

# Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly

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## Summary

1. Functional traits and phylogeny offer different, and often complementary, information about ecological differences between species, an essential step to uncover biodiversity assembly mechanisms and their feedbacks to ecosystem functions. However, traits and phylogeny are often related due to underlying trait evolution. Consequently, when combined, their shared information can be overemphasized, hindering their complementarity. It is therefore desirable to decouple their unique and overlapping contributions.

2. We propose a conceptual and mathematical framework that produces a set of meaningful measures of ecological differences between species.

3. We test the properties of these measures and the validity of the approach with extensive simulated data to show (i) the information provided by decoupling traits from phylogeny and vice versa, and (ii) that decoupling trait and phylogenetic information can uncover otherwise hidden signals underlying species coexistence and turnover. The application of the approach is further illustrated using a large dataset of Central European meadows as a case study.

4. Decoupling traits and phylogeny particularly reveals the importance of differentiation between phylogenetically related species, which can be essential to understand species replacements along environmental gradients and the combined action of environmental filtering and limiting similarity within communities.

5. Decoupling traits and phylogeny provides an avenue for connecting macro-evolutionary and local factors affecting coexistence and for understanding how complex species differences affect multiple ecosystem functions. We present an R function called ‘decouple’, which allows a simple and wide application of the framework.

**Key-words:** biodiversity, coexistence, ecosystem function, environmental filtering, limiting similarity, multivariate analyses, neutral theory, null models, phylogenetic corrections

## Introduction

Ecology has repeatedly considered species' ecological differences to understand the processes generating and maintaining biodiversity (Hutchinson 1959; MacArthur & Levins 1967; Diaz & Cabido 2001; Cornelissen *et al.* 2003; Losos & Ricklefs 2009). In recent decades, a growing demand to elucidate patterns of species assembly and biodiversity effects on ecosystem services has boosted the development of methods and studies focusing on species' ecological differences (McGill *et al.* 2006; de Bello *et al.* 2010; Connolly *et al.* 2011; Gerhold *et al.* 2015). Many of these approaches describe organisms' differences in

terms of functional traits, i.e. phenotypic attributes that can be linked to fitness and effects on ecosystems (Violle *et al.* 2007). An alternative, and potentially complementary, approach to capture species ecological differences considers the evolutionary distance between species (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Cadotte, Albert & Walker 2013; Gerhold *et al.* 2015).

The accumulation of available trait data has allowed using trait-based approaches for an increasing number of organisms, regions, and research questions (McGill *et al.* 2006; de Bello *et al.* 2010; Kattge *et al.* 2011; Weiher *et al.* 2011). Nevertheless, sufficient trait information for a large number of species and organism types is still lacking (Hortal *et al.* 2015). Even for well-studied groups (e.g. plants, Kattge *et al.* 2011), the traits that are most often measured are generally the easiest to

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collect, rather than the most 'functional' ones (Hortal *et al.* 2015). Moreover, differences between species are manifested via multiple traits (Cornelissen *et al.* 2003). This multidimensionality has effects on species coexistence (Kraft, Godoy & Levine 2015) and ecosystem functions (de Bello *et al.* 2010). Accordingly, several approaches have been proposed to select the most important traits and combine them in meaningful ways (Grime 1998; Laliberte & Legendre 2010; Laughlin 2014; Carmona *et al.* 2016). Still, potentially important or complex traits could be overlooked or remain difficult to measure, whereas uninformative or redundant traits could be included, thus diminishing our ability to adequately quantify biological differences between species.

An approach to account for missing or complex trait information is to use phylogenetic differences between species (Connolly *et al.* 2011; Cadotte, Dinnage & Tilman 2012; Penone *et al.* 2014; Lososová *et al.* 2015). The strength of the phylogenetic approach lies in the fact that it can provide a proxy for relevant functional traits, provided that traits possess a strong phylogenetic signal (Kraft *et al.* 2007; Cadotte, Dinnage & Tilman 2012; de Bello *et al.* 2015; Gerhold *et al.* 2015). Phylogenetic signal is high when ecological differences between species are proportional to the amount of time since they diverged from a common ancestor (Harvey & Pagel 1991; Webb *et al.* 2002). In practice, however, differences between species in terms of traits and of phylogeny often do not follow the same patterns (Swenson & Enquist 2009), even when traits possess a high phylogenetic signal (Mason & Pavoine 2013; Pavoine *et al.* 2013).

Using either trait or phylogenetic information in isolation could present various drawbacks in community and macroecology analyses (Cadotte, Albert & Walker 2013; Gerhold *et al.* 2015; Hortal *et al.* 2015). Accordingly, a combination of these two aspects of species differentiation has been encouraged (Kraft *et al.* 2007; Prinzing *et al.* 2008; Pillar & Duarte 2010; Pavoine *et al.* 2011; Diniz-Filho *et al.* 2012; Cadotte, Albert & Walker 2013). Unfortunately, it is still unclear to which extent such a combination can adequately reflect species ecological differences. Traits and phylogeny are often related due to underlying trait evolution (Webb *et al.* 2002; Münkemüller *et al.* 2012), meaning that the information they provide is not independent. Ideally, combining traits and phylogeny should allow consideration of both overlapping and unique information provided by each component (Fig. 1). Here we propose a conceptual and mathematical framework to quantify different aspects of species ecological differences, effectively allowing the combined use of species' functional and phylogenetic information.

#### TOWARDS DECOUPLING FUNCTIONAL AND PHYLOGENETIC SPECIES' DIFFERENCES

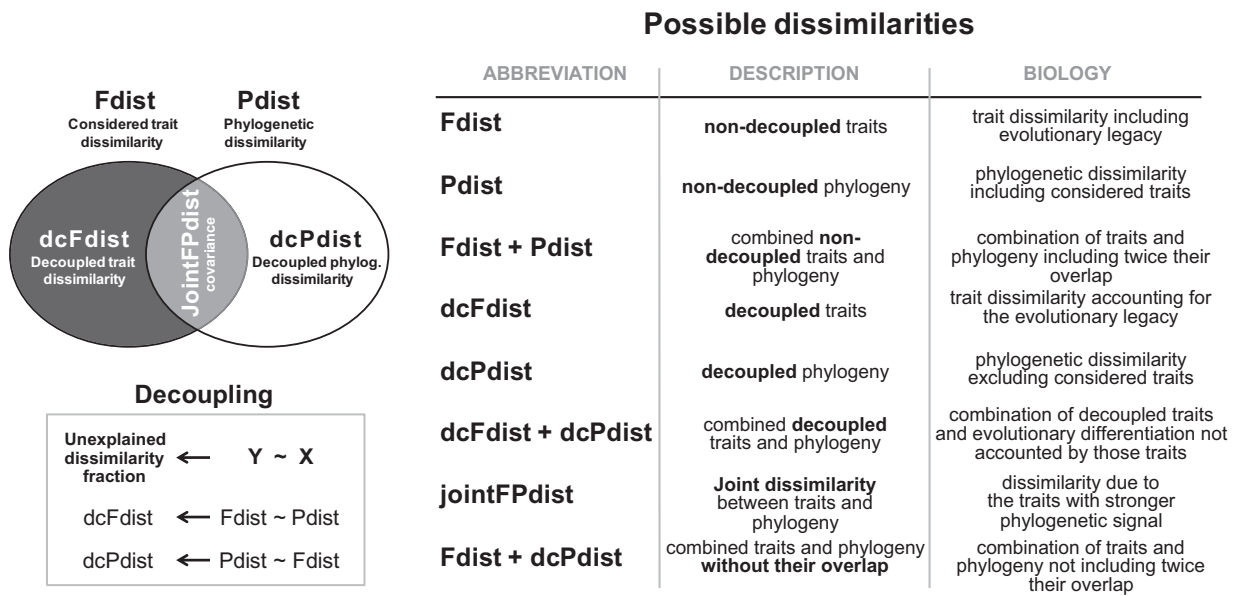
The potential of combining traits and phylogeny has fostered approaches considering both sources of information (Kraft *et al.* 2007; Prinzing *et al.* 2008; Pillar & Duarte 2010; Diniz-Filho *et al.* 2012). For instance, this has been attempted by comparing the information provided by functional and

phylogenetic data in combination with information about phylogenetic signal in trait evolution (Kraft *et al.* 2007; Prinzing *et al.* 2008; Swenson & Enquist 2009). It has also been proposed that functional and phylogenetic differences between species (**Fdist** and **Pdist** respectively) could be combined, resulting into a single comprehensive measure of species' pairwise differences (Cadotte, Albert & Walker 2013). The combination of Fdist and Pdist (termed 'phylogenetic-functional distance', or **PFdist**) is, simply put, a summation of trait and phylogenetic differences (Fdist + Pdist, Fig. 1). This combination can be weighted differently to account for various contributions of traits and phylogeny, for example to maximize the explanatory value for a response variable (Cadotte, Albert & Walker 2013).

Although the correlation between Fdist and Pdist is often weak, particularly when trait phylogenetic signal is low (Freckleton, Harvey & Pagel 2002; Mason & Pavoine 2013; Letten & Cornwell 2014), Fdist and Pdist are to some degree non-independent. The overlapping information between Fdist and Pdist, which can be represented by their joint dissimilarity structure (**jointFPdist**, Fig. 1), is the central caveat of combining functional and phylogenetic dissimilarities. This is because summing up Fdist and Pdist to combine functional and phylogenetic dissimilarity leads to jointFPdist being considered twice. When traits have high phylogenetic signal, resulting in redundant information of Fdist and Pdist, combining functional and phylogenetic dissimilarities will overemphasize the differences between distantly related species – with rather different traits – and diminish the differences between related species.

Accounting for phylogenetic legacy on traits has been a common approach in species-centred analyses relating species' environmental preferences to traits after removing the effect of phylogeny (Westoby, Leishman & Lord 1995; Blomberg & Garland 2002; Desvignes *et al.* 2003). As species are not phylogenetically independent from each other, it is common practice to use methods 'correcting' this dependence (Pagel 1999; Revell 2009; Diniz-Filho *et al.* 2012; de Bello *et al.* 2015). However, phylogenetic relatedness between species is being increasingly considered not only as a bias to be corrected, but as an evolutionary signal allowing description of patterns and inference of processes at different evolutionary scales (Cavender-Bares *et al.* 2009; de Bello *et al.* 2015; Gerhold *et al.* 2015). Remarkably, these methods are almost exclusively used for analyses relating species distributions or behaviour to traits, or traits to each other. Further developments could allow using this approach to study functional and phylogenetic biodiversity within and between communities (i.e. the extent of functional and phylogenetic differences between species; see Pavoine & Bonsall 2011 for a review).

However, it remains unclear how functional and phylogenetic components of species differences should be teased apart, particularly when multiple traits are considered together. Early attempts have assessed changes in community trait structure along environmental gradients after accounting for the effect of phylogeny (Pillar & Duarte 2010; Diniz-Filho *et al.* 2011; Pavoine *et al.* 2011). In these approaches, different matrices including traits, phylogeny, environmental and, sometimes,



**Fig. 1.** Possible approaches to define the extent of functional and phylogenetic differences between species and their combinations. Functional trait information can be used alone to compute functional dissimilarity between all pairs of species (Fdist). Phylogenetic information can be used alone to compute phylogenetic dissimilarity between all pairs of species (Pdist). These dissimilarity matrices can be combined as proposed by Cadotte, Albert & Walker (2013); Fdist + Pdist). However, Fdist and Pdist will at least partially covary together (greater covariance with greater phylogenetic signal in traits). To account for their independent (i.e. unique) components of dissimilarity, Fdist and Pdist can be decoupled (see Appendix S1 for a schematic summary of all steps involved; Appendix S4 for an R script). This decoupling provides functional trait differences independent from phylogeny (dcFdist) and phylogenetic differences independent from functional traits (dcPdist) and also a dissimilarity between species reflecting the covariance between traits and phylogeny (jointFPdist). All the matrices of species dissimilarity can be combined providing different types of measures. The main examples are provided in the table.

spatial data are combined (e.g. Pavoine *et al.* 2011). Although this has proven to be a useful approach to combine different types of data, it does not allow focusing directly on different measures of ecological dissimilarities, particularly traits decoupled from phylogeny as well as the shared information between traits and phylogeny. These sets of dissimilarities (Fig. 1) can be applied in a flexible manner in a variety of analyses as response variables or predictors. Focusing on unique and overlapping information between phylogeny and traits, and their combination is essential to understand species replacement along environmental gradients, the combined action of multiple assembly processes on communities, and how complex species differences affect ecosystem functions. In this direction, Diniz-Filho *et al.* (2011) proposed a promising approach using phylogenetic eigenvectors to estimate trait dissimilarity between species in the form of one trait decoupled from phylogeny. This approach can be effectively expanded to account for multiple traits and for defining measures that provide unique and overlapping functional and phylogenetic differences (Fig. 1).

In particular, existing approaches do not produce a measure of phylogenetic dissimilarity between species decoupled from functional trait information. An exception in this regard is the use of partial Mantel tests to evaluate whether phylogeny data significantly improves model fit when trait data are already included and vice versa (Violle *et al.* 2011). This useful idea, however, requires an *a priori*, external variable (to trait and phylogeny) against which partial effects are

tested, like in a Mantel test. More generally, it would be useful to assess functional differences between species independent from phylogeny (decoupled functional differences, **dcFdist**; Fig. 1), as well as phylogenetic information independent from functional traits (**dcPdist**). The former can provide a novel insight in community assembly patterns, particularly to focus on functional differentiation after accounting for the effect due to phylogeny (and therefore to focus on functional differentiation between more phylogenetically related species; de Bello *et al.* 2015). The latter would allow understanding the additional importance of phylogeny, and therefore potentially unexplored traits. Interestingly, while some authors recognize that phylogenetic information can complement traits, accounting for additional information such as unmeasured functions (Cadotte, Albert & Walker 2013; Gerhold *et al.* 2015), it is generally not acknowledged that phylogenetic information should be decoupled from the effect of traits already considered (but see Violle *et al.* 2011). We propose a conceptual and mathematical framework that presents a solution to these open challenges, producing a set of biologically meaningful measures of ecological differences between species (Fig. 1). Our approach is fundamentally different from a partitioning method, since it is not focused on partitioning phylogeny and trait differences into additive components. Rather, it produces objects that allow subsequent partitioning of unique and shared effects of phylogeny and traits in a variety of analyses. For this reason we refer to ‘decoupling’ here.

## Framework

### HANDLING PHYLOGENETIC AND TRAIT DATA

Two types of data are needed to apply the framework: phylogenetic relationships among species and their functional traits. For phylogeny the input data are a phylogenetic tree, which can be built in different ways, or retrieved from different sources (Webb *et al.* 2002). The traditional output from the phylogenetic tree is a distance matrix indicating how related pairs of species are (Pdist), usually representing evolutionary time since they separated from their most recent common ancestor. It is also possible to use directly a distance matrix computed from DNA sequences. In any case, it is necessary to decide whether to follow, or not, the suggestion by Letten & Cornwell (2014) to square-root these distances, which seems essential to reflect the cases where evolutionary relatedness is not linearly related to ecological distance between species (see also Hardy & Pavoine 2012). Other transformations to consider different types of evolutionary patterns are possible (Diniz-Filho *et al.* 2012).

Functional traits are generally provided as input data in the form of a species-by-traits matrix, from which differences are computed for each pair of species as output distance matrix (Fdist). Different types of distance measures can be used for both continuous and categorical traits to calculate standardized distances between species in multidimensional trait space (Laliberte & Legendre 2010; de Bello *et al.* 2013; Carmona *et al.* 2016). It is worth noticing that accounting for intraspecific trait variability is also possible with the approach, e.g. by using trait overlap in hypervolumes or trait probability density curves to estimate pairwise dissimilarity between species (Carmona *et al.* 2016).

### DECOUPLING

To obtain trait information decoupled from phylogeny we employ a model in which the phylogeny (in form of eigenvectors from a principal coordinate analysis, see below) is used as explanatory variable and traits as response variables (Fig. 1 and, for a scheme of all steps involved in the framework, see Appendix S1, Supporting Information). The unexplained part of that model (i.e. the residuals) is taken as the variation in species' traits decoupled from phylogeny, i.e. trait variation independent from phylogeny. The explained part represents the information shared (overlapping) between traits and phylogeny. We then use an analogous approach to obtain phylogenetic distances decoupled from the available trait information. The data used and generated in these steps is eventually used to calculate different distance matrices (Fig. 1).

To be able to use the phylogeny as predictors of traits, the matrix of phylogenetic distances must be expressed as coordinates of the space that those distances span. These coordinates (phylogenetic eigenvectors, Diniz-Filho *et al.* 2012; Guenard, Legendre & Peres-Neto 2013) are calculated using principal coordinate analysis (PCoA; called 'species PCoA scores' in Appendix S1). The set of phylogenetic eigenvectors must be

reduced, because using all eigenvectors to explain the traits would result in a saturated model (see also Desdevises *et al.* 2003). The reduction is based on how well individual eigenvectors contribute to predicting trait values. Accordingly, a linear regression model for each trait is selected that finds a minimum adequate subset of predictors among eigenvectors. All phylogenetic eigenvectors that significantly explain the variation in at least one trait are retained ('Reduced PCoA eigenvectors'; Appendix S1).

The reduced set of phylogenetic eigenvectors can be used in combination with single traits as proposed by Diniz-Filho *et al.* (2011), who used the species phylogenetic PCoA eigenvectors as predictors of trait values. The residuals from this model reflect 'unique' variation in a trait, excluding the overlapping information of that trait and phylogeny (dcFdist, Fig. 1). The fitted values represent the overlapping information between the trait and phylogeny (jointFPdist, Fig. 1). Using multivariate analyses instead of linear regression allows the approach to be extended to multiple traits, and also to be used to decouple phylogenetic diversity from trait diversity (with the assumptions of linear relationship between traits and phylogeny maintained by square rooting of phylogenetic distances for possible nonlinear evolutionary process, see Letten & Cornwell 2014; although further research is needed to verify this assumption). The natural choice for the multivariate method is redundancy analysis (RDA), which summarizes both the variation in response data fitted by the predictors and the residual variation (Legendre & Legendre 2012). This analysis produces two types of species scores:

**1** The species scores on the predictors' axes (called 'constrained' axes) are the fitted values, which represent the variation in functional traits explained by the phylogeny. These scores represent shared variation between traits and phylogeny and can be used to compute the dissimilarity matrix (jointFPdist).

**2** Species scores on residual axes (often called 'unconstrained' axes) represent the variation not accounted for by model predictors. Thus they can be used to compute a distance matrix reflecting species differences in terms of traits not accounted for by phylogeny (dcFdist).

Note that within each set of constrained and unconstrained axes, the axes are ordered from more to less important by decreasing eigenvalues, which quantify the amount of variation explained in the data. We suggest computing a weighted Euclidean distance, with scores of each axis weighted by its corresponding eigenvalue, to estimate species dissimilarity.

This approach can also be used to produce phylogenetic differences decoupled from the traits (dcPdist) by taking species scores on unconstrained axes of RDA with all phylogenetic PCoA eigenvectors used as response variables and all traits as predictors. While in principle jointFPdist could be calculated using either analysis, we suggest using the RDA with traits as response variables to compute it. In fact, we cannot use a single trait as a predictor of phylogeny because the RDA species' scores would be just rescaled values of that trait. The problem will be similar even when combining multiple traits. Because of the different ways to constrain the analyses, the approach is, by

essence, not symmetrical. The two-way decoupling provides unique contributions of functional and phylogenetic dissimilarities, and this is achieved despite this asymmetry.

An advantage of our approach is that the decoupling allows for extracting unique and overlapping information for further uses in testing community structure effects. This avoids the problem of using only the residuals of one variable over the other and not together, as stressed by Freckleton (2002), for example in the context of Mantel tests. It is important to notice that the selection of eigenvectors raises some concerns (Freckleton, Cooper & Jetz 2012), because it might lead to overly liberal selection of predictors and consequently overestimate the relative contribution of phylogeny. This issue, however, will occur only if traits are strongly correlated, because trait correlations create redundancy of selected predictors (eigenvectors). To account for this, trait correlations can be estimated before running the decoupling procedures, to remove redundant traits. Alternatively we suggest applying a variant of the approach, based on a single step selection using RDA, adopting stopping criteria suggested by Blanchet, Legendre & Borcard (2008). This involves (i) calculating RDA with all eigenvectors as predictors and estimating the size of adjusted  $R^2$  (explained variation); (ii) performing stepwise selection based on adjusted  $P$  values (using either Holm correction or false-discovery-rate based selection); (iii) stopping either at the first  $P$  value exceeding a given threshold or when the addition of the next best predictor leads to a model with adjusted  $R^2$  greater than the adjusted  $R^2$  calculated with all eigenvectors, see (i) above.

Notice that with our approach it is also possible to summarize the amount of overlapping information between traits and phylogeny with a simple index. In this sense the total variation in traits explained by phylogeny can be set up as a reference. In terms of the figure in Appendix S1, explaining the whole procedure, this corresponds to comparing the variation in dcFdist

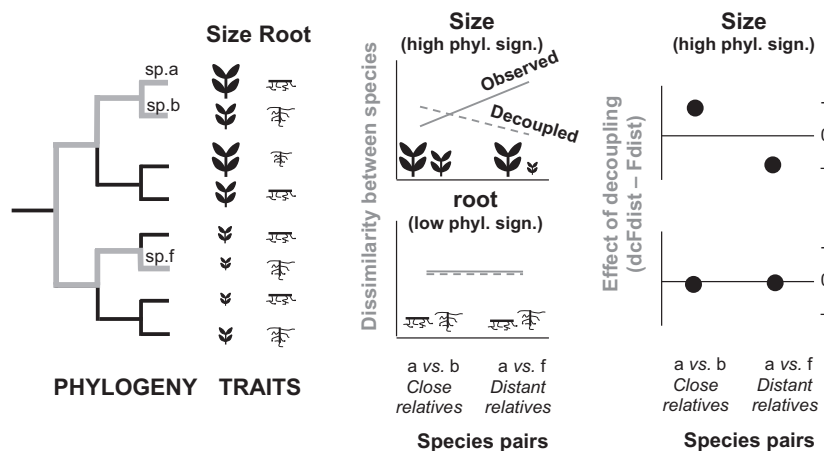
and jointFPdist. This can be done in the RDA by checking how much variation in traits is explained by the selected phylogenetic eigenvectors (and we specifically suggest using adjusted  $R^2$ ).

## Simulations

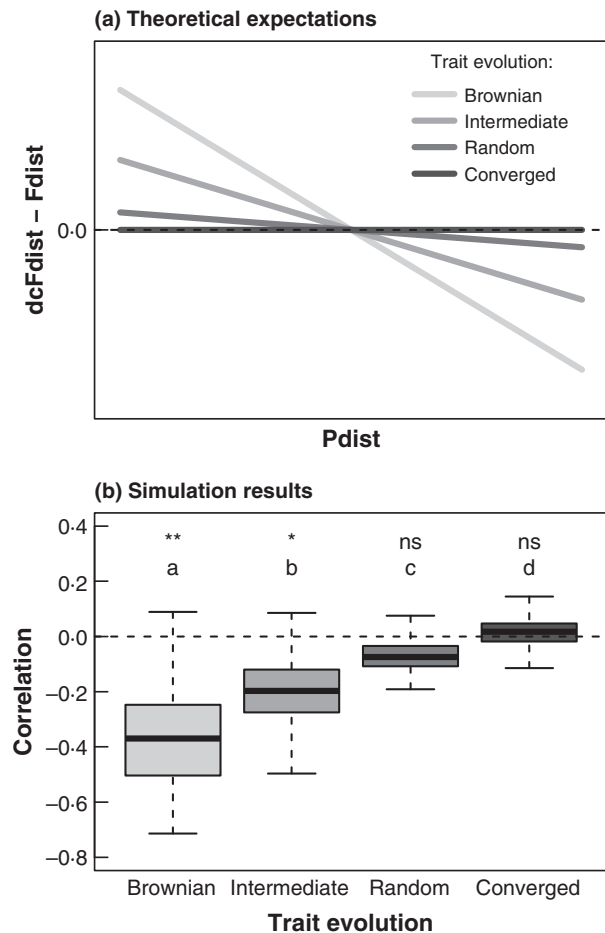
We tested the decoupling approach using simulated communities assembled according to different species sorting processes. We first assessed the effects of decoupling on traits given different trait evolution scenarios (test 1). Then, though the approach proposed can be used for several applications, we illustrate its advantages in the study of species coexistence patterns (tests 2 and 3). Based on Münkemüller *et al.* (2012), we generated for all tests different trait evolution scenarios, from Brownian motion to convergent evolution, i.e. with stronger to weaker phylogenetic signal. The data generated in these scenarios were then combined with existing community simulation approaches (Kraft *et al.* 2007) for tests 2 and 3. We did this to account for the potential applications of the framework, including the case of combining functional and phylogenetic information with missing trait information. These three tests are described in detail in the following sections. Due to space limitations we give additional details of the involved simulations in Appendix S2.

### TEST 1: EFFECT OF DECOUPLING

Our expectations for this test are summarized in Figs 2 and 3. When the phylogenetic signal of traits is high, the overlapping information between traits and phylogeny is high (e.g. 'size' trait in Fig. 2). In this case, functional differences within clades (e.g. species 'a' vs. species 'b'), which are originally low, should increase. On the contrary, differences between clades (e.g. species 'a' vs. species 'f') should decrease. Consequently, the



**Fig. 2.** Expected changes in trait dissimilarities between species pairs with decoupling. A theoretical example with 8 species and 2 traits, plant size and root type. Plant size represents, in the example, a trait with high phylogenetic signal (i.e. 'phyl. sign.' in the figure). Changes in dissimilarity are shown for the two pairs of species: species 'a' vs. species 'b' and species 'a' vs. species 'f'. For each of the panels on the right side of the figure, the observed dissimilarity (using the observed trait values or phylogeny) is compared to the dissimilarity obtained after decoupling. The difference between the two (dcFdist – Fdist) is then used to show the effect of simulation in Fig. 3. Notice that for traits with high phylogenetic signal (plant size in the example), the two lines in the upper left panel might not always intersect and that in some cases the 'decoupled' line might be horizontal.



**Fig. 3.** Test 1: (a) Theoretical expectations of decoupling effects depending on trait evolution patterns and the phylogenetic dissimilarity (Pdist) between species (see also Fig. 2). The decoupling should cause larger effects with greater phylogenetic signal of traits because of a greater overlap between functional and phylogenetic information. In this case the difference between decoupled and non-decoupled functional differences (i.e. dcFdist minus Fdist) should increase between closely related species and it should decrease between more distantly related species (see also Fig. 2). (b) Results of the simulations (1000 trait evolutions for each trait evolution patterns) showing the effect of decoupling between functional and phylogenetic differences. For each simulation the correlation between the Pdist and dcFdist – Fdist was calculated (following panel ‘a’). Within each trait conservatism scenario, the proportion of simulations where this correlation was not smaller than zero was used to test whether decoupling had an effect on the changes in functional dissimilarity (\*\* $P < 0.01$ ; \* $P < 0.05$ ; ns  $P > 0.05$ ). In addition, we performed an ANOVA, followed by a Tukey post hoc test to reveal differences in the effect of decoupling between the different trait conservatism scenarios (different letters indicate significant differences between scenarios at the  $P = 0.05$  level). For more results, including combination of different traits, see Appendix S2.

difference between decoupled functional dissimilarity and standard functional dissimilarity (dcFdist – Fdist) should be positive for more closely related species and negative for less closely related species when traits are more related to phylogeny. For traits with low phylogenetic signal (e.g. root type in Fig. 2), the effect of decoupling should be negligible. To assess these predictions we tested, for each simulation, the

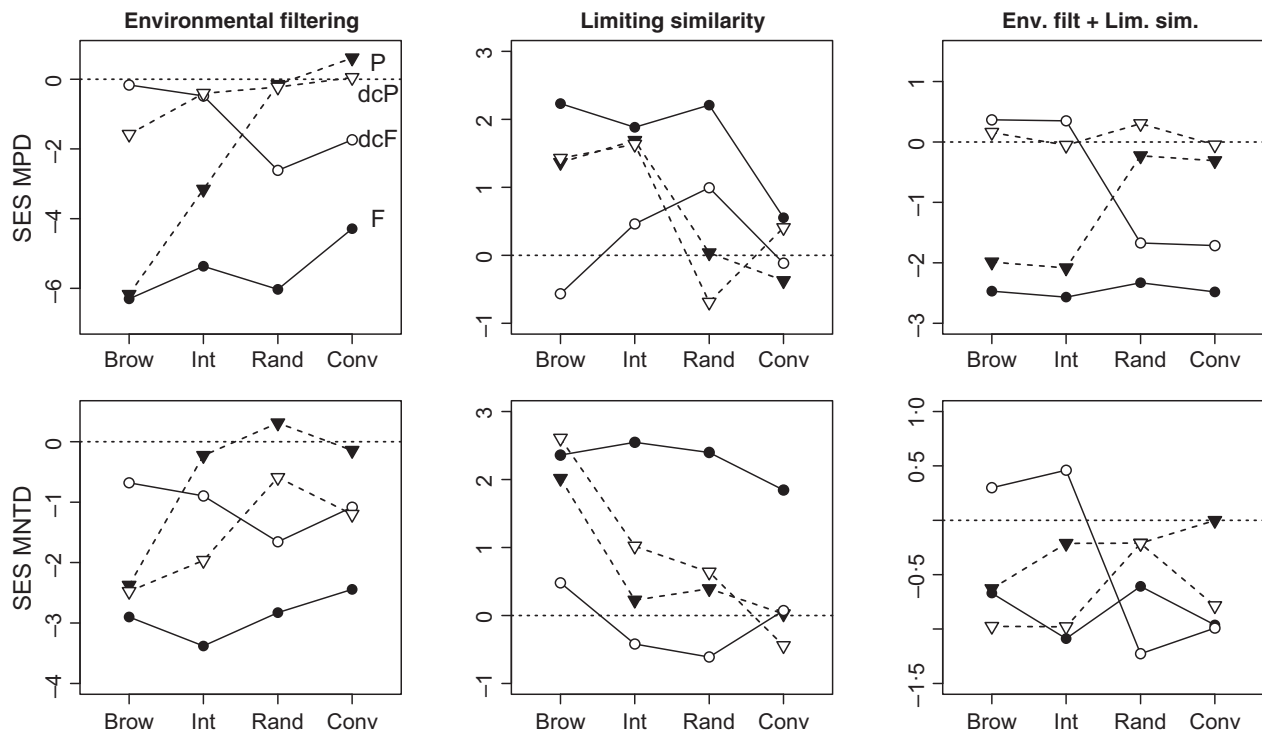
correlation between changes in trait dissimilarity with decoupling (dcFdist-Fdist) and phylogenetic dissimilarity between species pairs (which corresponds to the way Mantel  $r$  is calculated). The theoretical expectation in the case of high phylogenetic signal in traits is a negative correlation between Pdist and dcFdist-Fdist.

The simulations showed that the decoupling approach indeed magnified the differences between more closely related species, by focusing on within- rather than between-clade trait differences. The greater phylogenetic signal in traits, the more the functional difference between closely related species increased with decoupling (positive difference between dcFdist and Fdist) and the more the functional difference between less related species decreased with decoupling. This effect progressively vanished as the phylogenetic signal decreased, up to the point that decoupling did not cause any differences between groups with lowest phylogenetic signals (Fig. 3). Combining traits provided similar results, i.e. the larger the extent of trait phylogenetic signal in the ensemble of traits, the greater was the effect of decoupling (Appendix S2).

#### TEST 2: DETECTION OF ASSEMBLY PATTERNS: ONE TRAIT CASE

Following test 1, we expected that decoupling would prove particularly useful to detect cases of community assembly in which functional differentiation between closely related species is important for species coexistence. We considered four scenarios of assembly processes operating on species sorting following Kraft *et al.* (2007) and considering the four trait evolution scenarios of test 1. In particular we considered communities assembled (i) randomly, (ii) by functionally similar species (environmental filtering), (iii) by functionally different species (limiting similarity) and (iv) by the combination of (ii) and (iii). These assembly scenarios sorted 15 species, out of a pool of 50, based on the trait value of one trait. For each generated community we calculated indices of functional and phylogenetic diversity (mean pairwise dissimilarity, MPD, and mean nearest-taxon diversity, MNTD; Weiher, Clarke & Keddy 1998; Pavoine & Bonsall 2011; Lososová *et al.* 2015) from decoupled (dcFdist and dcPdist) and non-decoupled (Fdist and Pdist) dissimilarities. We then compared the observed values of MPD and MNTD against those obtained from the random assembly scenario (Kraft *et al.* 2007). To do so, we used standardized effect size (SES), i.e. observed diversity minus mean random values all divided by the SD of random values (SES values lower than zero indicate diversity being lower than random and vice versa for SES values above zero). See Appendix S2 for more details.

The results (Fig. 4) generally show that non-decoupled measures of dissimilarity produced expected patterns for environmental filtering and limiting similarity (SES  $< 0$  and SES  $> 0$  respectively) but failed to detect the importance of differentiation between functionally similar and closely related species in the case of combined environmental filtering and limiting similarity. Functional dissimilarity (Fdist) provided results largely independent on the evolution of the trait and reflected the type



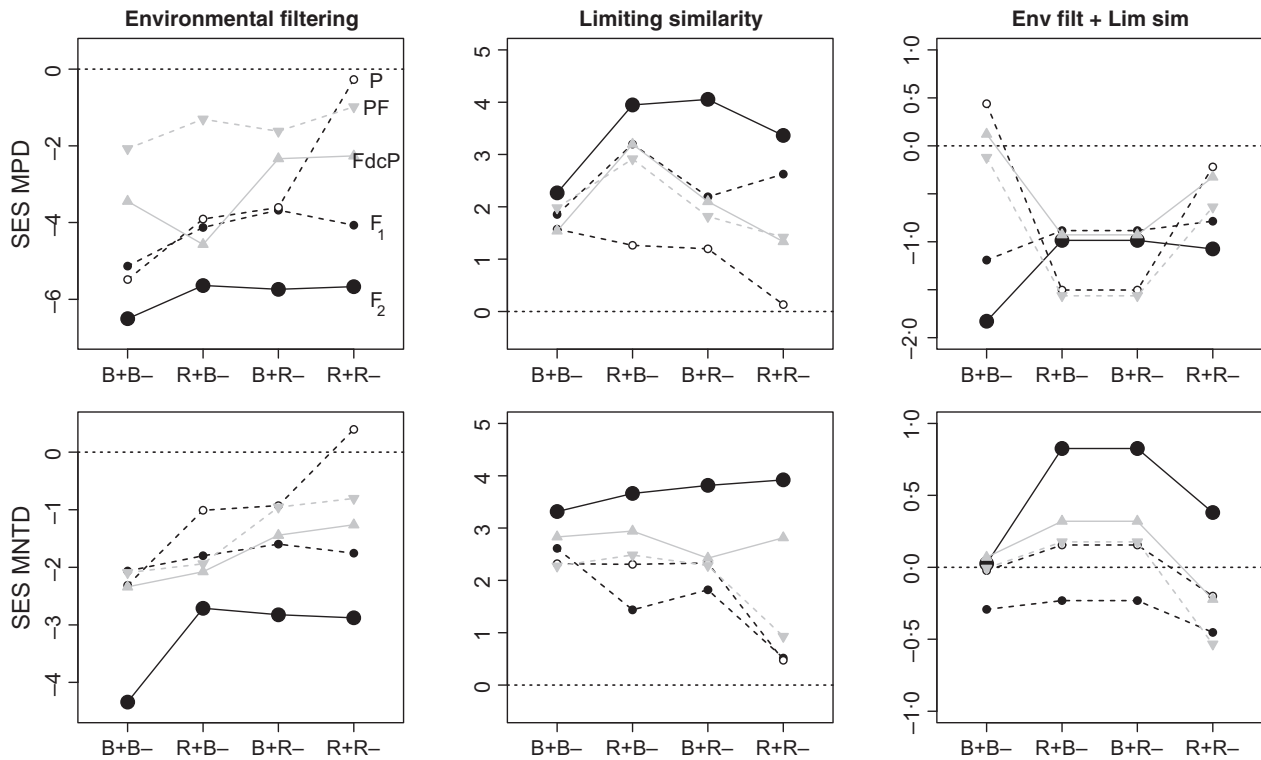
**Fig. 4.** Test 2: detection of assembly patterns (environmental filtering, limiting similarity and their combination) depending on trait evolution scenarios (Brow, Brownian motion; Int, intermediate between Brownian motion and random; Rand, random; Conv, convergent evolution). The test is done using various dissimilarity measured, either decoupled (dcF, decoupled functional dissimilarity; dcP, decoupled phylogenetic dissimilarity) or not (F, functional dissimilarity; P, phylogenetic dissimilarity). For each of these combination two indices of diversity were computed, i.e. MPD and MNTD and compared to random assembly using standardized effect size (SES), with  $SES > 0$  indicating indices being greater than random values and vice versa. Points indicate the mean SES value for each combination of scenarios (error bars were most of the time too small to be visible).

of assembly rules simulated. Only when the trait considered in the simulations had a high phylogenetic signal, using phylogeny dissimilarity (Pdist) gave similar results to using Fdist. This confirms existing studies showing that phylogenetic diversity can be used as a proxy of functional diversity only when the traits have a considerable phylogenetic signal (Kraft *et al.* 2007; Swenson & Enquist 2009; Lososová *et al.* 2016) although even in this case such proxy might not be ideal (Mason & Pavoine 2013). Importantly, the scenario with the combination of environmental filtering and limiting similarity gave values significantly lower than random values (with a one-sample *t*-test), generally confirming the difficulty to detect limiting similarity when also environmental filtering is operating (Götzenberger *et al.* 2016).

Most interestingly, with decoupled dissimilarity (dcFdist), SES values for a scenario combining environmental filtering and limiting similarity tended consistently to be above zero and different from random expectations, in the case of Brownian evolution and intermediate phylogenetic signal (one-sample *t*-test  $P < 0.05$ ; see Appendix S2 for a discussion on significant departure of SES values). SES above zero for dcFdist is an interesting result corresponding to the expected frequent case in which communities are assembled by opposing processes operating on the same trait. For instance, environmental filtering may select species of few clades with similar traits; then, within these clades, limiting similarity selects for functionally different species. Using null-models with Fdist

and Pdist separately cannot reveal the signature of these opposing assembly forces, when they act on the same trait (Götzenberger *et al.* 2016). Only with decoupling one obtains SES values greater than expected by random assembly, thus effectively detecting a signal of limiting similarity within a pool of species already filtered by environmental conditions.

It should be noticed that phylogenetic information decoupled from trait information (dcPdist) provided some apparently counterintuitive results. The aim of this decoupling is to 'remove' the information of traits already considered from phylogeny, but the decoupling of phylogeny from traits (dcPdist) was found partially correlated with trait dissimilarity, even in case of highest phylogenetic signal (Mantel test  $P < 0.05$ , although the correlation was generally low, i.e. Mantel  $r = 0.15$ ). Therefore, in some of the simulations dcPdist followed the patterns of Pdist rather than showing absence of patterns ( $SES \sim 0$ ). We attribute this effect to the lack of high complexity in the example (having 50 species and 1 trait). Decoupling phylogeny from traits could prove limited when using only one trait and few species as it is challenging to find a single predictor for all phylogeny axes considered in such cases. As a matter of fact, by increasing the complexity of the example, e.g. by increasing the number of species 100 or 200, this effect vanished (i.e. SES was consistently around zero and no correlation between dcPdist and Fdist), showing that the problem will only exist in over-simplified datasets.



**Fig. 5.** Test 3: detection of species sorting processes (see Fig. 4 for more details) depending on the amount of trait information available and depending on which trait is available and which is missing. Functional diversity computed with two traits ( $F_2$ ) represents the ‘control’, as assembly was based on the combined dissimilarity of the two traits. Other cases consider: (i) using the functional dissimilarity of only one of the two traits ( $F_1$ ), (ii) the phylogenetic distances only ( $P$ ) (iii) a combination of 1 trait with phylogeny (i.e.  $Pdist + Fdist$ , here named ‘PF’ due to space limitation) and (iv) a combination of 1 trait with the decoupled part of phylogeny from the trait already considered ( $Fdist + dcPdist$ , here named ‘FdcP’). Four cases of traits with different evolution patterns were considered: (a) combination of two traits evolved according to Brownian motion ( $B+B-$ , indicating one trait being available and the other not); (b) a combination of two traits with random evolution ( $R+R-$ ) and, finally, the combination of the two types, with either the Brownian trait missing ( $R+B-$ ) or the random trait missing ( $B+R-$ ).

#### TEST 3: DETECTION OF ASSEMBLY PATTERNS: TWO TRAITS CASE

We assessed how phylogenetic information could be used to estimate missing trait information by comparing diversity measures computed with two known traits against a number of alternatives: (i) using  $Fdist$  of only one of the two traits (i.e. information for one trait missing), (ii) the phylogenetic distances ( $Pdist$ ) only (two traits missing), (iii) a combination of one trait with phylogeny (i.e.  $Fdist + Pdist$ , following Cadotte, Albert & Walker 2013, with  $Fdist$  and  $Pdist$  having the same contribution), and (iv) a combination of one trait with the phylogeny decoupled from trait information ( $Fdist + dcPdist$ ). To take into account the effect of different trait evolution, we considered four combinations of the two traits, with the available trait either evolved under Brownian motion or under random evolution, and the same scenarios for the missing trait.

It is interesting to notice that using only one trait (out of the two involved in simulated assembly) was often better, or comparable, to using phylogeny or combining one trait and phylogeny, even though traits were not correlated (Fig. 5). This happened in all cases except when both traits evolved under Brownian motion. When using phylogeny instead of traits, or phylogeny combined with one trait, predictions worsened when the missing traits had no phylogenetic signal in the

missing trait, in this case. This shows that results will be ambiguous when irrelevant information about the dissimilarity between species is considered (either phylogeny unrelated to the missing traits or potentially a trait not relevant to the question being asked). Generally the existing approach of combining  $Fdist + Pdist$  without decoupling provided less negative SES values in the environmental filtering scenario (lower detectability). It also gave lower values in limiting similarity and under the combination of environmental filtering and limiting similarity (with the exception for MPD with two traits evolved under Brownian motion). Notice also that only by using  $Fdist + dcPdist$  the SES values were consistently (and significantly) above zero, for both MPD and MNTD, when environmental filtering and limiting similarity acted in concert. Again, this shows the importance of decoupling to detect assembly patterns caused by the combination of environmental filtering and limiting similarity.

#### Discussion

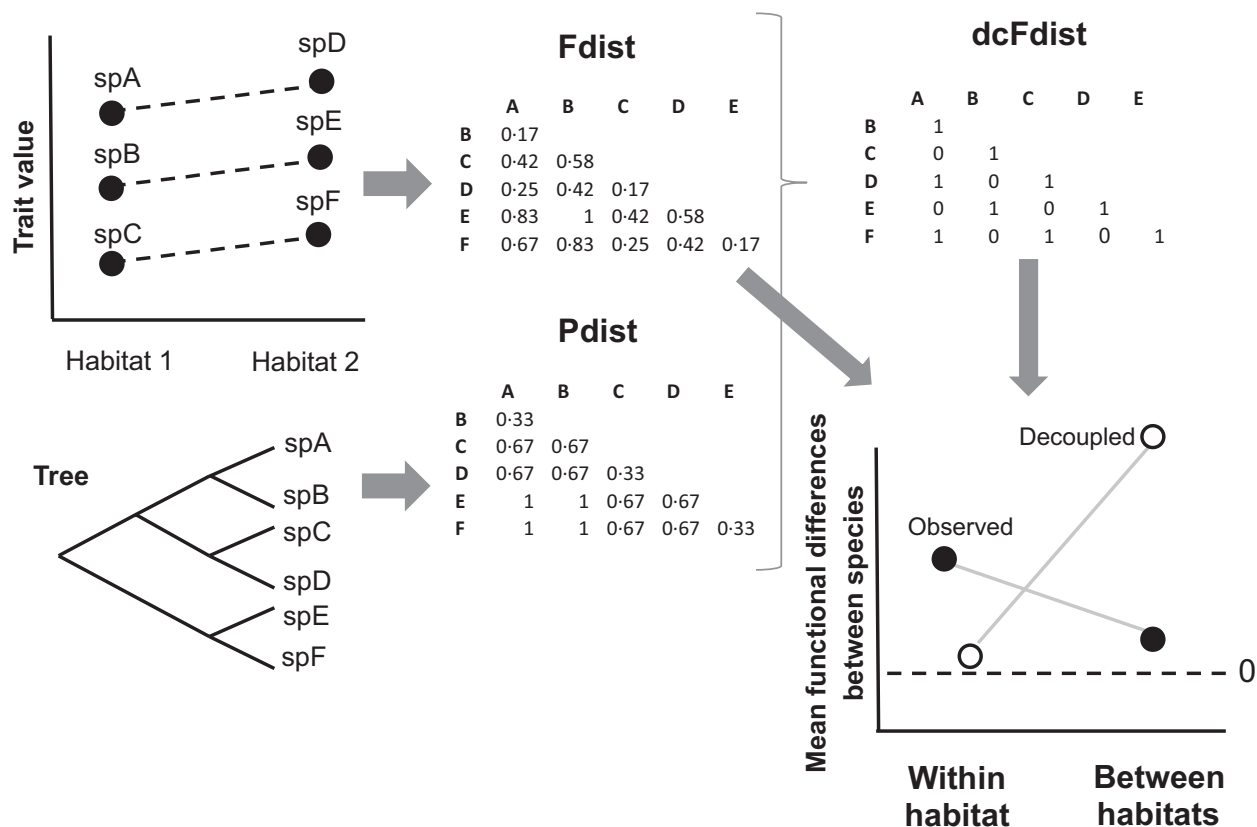
The proposed framework opens an avenue for connecting macro-evolutionary and local ecological factors affecting community assembly, and for understanding how complex differences between species affect ecosystem functions. While validating the approach the simulations revealed that

**Table 1.** Application of the decoupling with null-models, following test 2, on a real case study

	N	SES MPD			SES MNTD		
		Mean	Mean <sub>dec.</sub>	P between means	Mean	Mean <sub>dec.</sub>	P between means
<b>Functional</b>							
LHS	293	-0.38***	0.19**	<0.001	0.04	-0.13*	<0.05
LHS & Clonality	293	-0.58***	-0.31***	<0.01	-0.29***	-0.31***	0.859
Height	293	-1.01***	-0.17	<0.001	-0.77***	0.15*	<0.001
Clonality	179	-1.01***	0.20	<0.001	-0.67***	0.20**	<0.001
SLA	293	-0.77***	0.69***	<0.001	-0.23***	0.84***	<0.001
Seed mass	293	-0.67***	-0.31***	<0.001	-0.39***	-0.21***	<0.05
<b>Phylogenetic</b>							
LHS	293	-1.23***	0.22	<0.001	-1.33***	-1.03***	<0.001
LHS & Clonality	293	-1.08***	-1.02***	0.595	-1.34***	-0.82***	<0.001
Height	293	-1.05***	-0.53***	<0.001	-1.34***	-1.27***	0.507
Clonality	179	-1.12***	-1.06***	0.715	-1.20***	-1.28***	0.527
SLA	293	-1.02***	-0.51***	<0.001	-1.27***	-1.07***	<0.05
Seed mass	293	-1.13***	0.14	<0.001	-1.35***	-1.04***	<0.001

Mean values of the standardized effect sizes of mean pairwise distances (SES MPD) and mean nearest-taxon distances (SES MNTD), calculated from functional and phylogenetic distances matrices, for a given trait or trait combination. 'N' represents the number of plots of wet meadows for which sufficient trait data were available. In the table 'mean' represents the value based on 'pure' functional and phylogenetic distances, whereas 'mean<sub>dec.</sub>' represents the values based on the decoupled functional and phylogenetic distances. Asterisks behind the means indicate the means significantly different from zero in a two-tailed *t*-test for a single sample. 'P between means' represents a two sample *t*-test of difference between means for pure and decoupled distances. LHS, leaf-height-seed combination of traits. Note that SES values for Phylogeny ('Mean') can vary a little depending on the randomisation.

\*\*\**P* < 0.001; \*\**P* < 0.01; \**P* < 0.05.



**Fig. 6.** Illustrative case in which the functional turnover between habitats is mostly occurring within pairs of closely related species (e.g. spA and spB). In such case, using the observed functional dissimilarity (undecoupled) would result in within-habitat dissimilarity to be, on average, larger than between-habitat dissimilarity. Decoupling, on the contrary, reveals the pattern of within-clades differentiation by increasing the relative size of between-habitats differentiation.

decoupling provides additional insight into community assembly. By decoupling the unique and overlapping information contained in trait and phylogenetic differences between species, we can highlight the importance of local species differentiation for coexistence even if environmental filtering is operating on community assembly. Such local differentiation can remain undetected by the prevailing effect of environmental filtering (Götzenberger *et al.* 2012, 2016), particularly when environmental filtering acts on traits with high phylogenetic signal. In this case, the prevailing larger-scale phylogenetic signal leads coexisting species to be both evolutionary and functional subsets of the regional species pool. Decoupling, on the contrary, can help uncover potential patterns of local differentiation within this clustered pool of species, e.g. differentiation within groups of congeneric or closely related species.

A real dataset illustrates a case of such prevailing environmental filtering masking local differentiation patterns, and how decoupling can uncover such differentiation patterns. The case study (a large dataset of species rich mesic meadows from Central Europe; see details in Appendix S3) showed negative values of SES for both traits and phylogeny (Fdist and Pdist). This indicates that coexisting species tended to be evolutionary close (i.e. from related clades) and functionally similar, possibly through overlapping information between traits and phylogeny. On the contrary the SES values for functional diversity based on decoupled measures of dissimilarity (dcFdist) showed several values being significantly positive (Table 1 and Appendix S3). The increase in functional diversity by decoupling indicates that closely related species coexist and differentiate within clustered communities. These patterns suggest that decoupled distances between species can reveal otherwise hidden signals in community structure. In particular, decoupling gave more importance to local species differentiation, so that within a 'filtered' set of more similar species there could be some significant differentiation, for example via a relatively more recent trait differentiation within closely related phylogenetic taxa, via character displacement or trait assortment (Webb *et al.* 2002; Prinzing *et al.* 2008; Losos & Ricklefs 2009).

Decoupling can also be used to study patterns of beta diversity, or in functional turnover between plots or habitats (Pillar & Duarte 2010; Siefert *et al.* 2013), which could be now performed with and without decoupling, as well as combining functional and phylogenetic dissimilarity without their overlap. This can be useful, for example, when species functional differentiation across habitats is due to replacement of functionally different species from the same clades (Fig. 6), like changes in body size along latitude, or when traits vary across habitats mostly within a genus (Hoffmann & Franco 2009; Revell 2009; Diniz-Filho *et al.* 2011; de Bello *et al.* 2015). It is important to notice that in this scenario decoupling is essential to reveal the effect of turnover on traits, which would be masked by phylogenetic clustering resulting from particular patterns of trait evolution. In this case, as in the other cases described in this study and elsewhere (de Bello *et al.* 2015), we do not recommend using only decoupled measures, but

comparing decoupled and un-decoupled estimations to gain new insights into community assembly patterns.

Decoupling can also provide a practical tool to determine the amount of missing and complementary information when using traits. By examining the importance of phylogenetic information decoupled from trait information (dcPdist), it is also possible to account for informative traits that have not been measured, or whose data are not available in existing trait databases. Combining traits and phylogeny has been proposed as a way to take full advantage of both sources of information in studies of community assembly (Cadotte, Albert & Walker 2013; Gerhold *et al.* 2015). Our results show, in this sense, that when the missing trait information has no strong phylogenetic signal, using phylogeny as complement of trait diversity is counterproductive and can lead to ambiguous results. Furthermore, our results show that it is reliable to combine directly trait and phylogenetic information mainly when jointFPdist is small. Consequently, before combining traits and phylogeny we recommend quantifying the importance of jointFPdist (see 'Decoupling' section above for methodological details). In the case of studied traits being correlated, decoupling among those traits (i.e. when one trait is decoupled from all other considered traits) could help understanding the unique contribution of individual traits to a given ecological function.

The strength of the proposed framework lies in its ability to estimate several new measures of ecological differences between species. We recommend to complement original measures of ecological dissimilarity with those suggested here (Fig. 1). The combination of these dissimilarity measures has an unexplored potential for assessing how species differences affect species assembly and, in turn, how this affects ecosystem functioning. To allow a simple and wide application of the framework we present an R function called 'decouple' (Appendix S4) further illustrated by some guided examples using simulations (Appendix S5).

## Authors' contributions

All authors contributed to the design of the methods and the writing of the text. L.G., C.M. and F.B. ran all analyses. L.G. designed the R function 'decouple' with the help of P.S. and F.B.

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## Data accessibility

The scripts to run the three tests in the Simulations section are provided in Appendix S2, Supporting Information. The data used in the case study in Table 1 derive from published and available data (see detailed references in Appendix S3).

Plant traits can be retrieved from the LEDA database (<http://www.uni-oldenburg.de/en/landeco/research/projects/LEDA/Data%20Files/>) and the CLOPLA database (<http://clopla.butbn.cas.cz/>). Phylogeny data can be retrieved from the DAPHNE database ([https://figshare.com/articles/Data\\_Paper\\_Data\\_Paper/3554421](https://figshare.com/articles/Data_Paper_Data_Paper/3554421)). Vegetation plots are extracted from the Czech National Phytosociological Database (<http://www.sci.muni.cz/botany/vegsci/dbase.php?lang=en>).

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Appendix S1.** Schematic summary of the procedures computing different types of dissimilarity between species following Fig. 1.

**Appendix S2.** Scripts and additional information for tests 1, 2 and 3 in the Simulations section.

**Appendix S3.** Additional information on the case study presented in Table 1.

**Appendix S4.** R functions, including the function ‘decouple’, to apply the framework proposed in this study.

**Appendix S5.** Example session with the ‘decouple’ function using simulated data.